Cranial size and shape variation, pelage and bacular morphology, and subspecific differentiation in spiny rats, *Proechimys albispinus* (Is. Geoffroy, 1838), from northeastern Brazil

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Abstract. The lack of unique and discrete character states that clearly diagnose the subspecies of *Proechimys albispinus* has undoubtedly contributed to the difficulty of assessing levels of differentiation and isolation and the systematic relationships within this species. Variation of color pattern in subapical zones of guard hairs, which has traditionally been used for diagnosis of subspecies, is quantitative and subtle. Although differences are apparent, by themselves they are not diagnostic, and the same is true for qualitative aspects of bacula and skull shape. In this study, cranial size and shape variation in three subspecies of Brazilian spiny rats, *P. albispinus*, was assessed by principal component (PC), discriminant function (DF), and size-free discriminant function (SF—DF) analysis of 18 characters measured on 133 individuals from 10 localities in the states of Bahia and Sergipe in northeastern Brazil. We originally hypothesized that the cranial morphometric data would support the previous designations of subspecies based on pelage and qualitative aspects of the skull observed by Moojen (1948). The morphometric analyses partially supported this hypothesis in that they show the almost complete discrimination of *P. a. minor* from the other two subspecies on the basis of cranial shape; however, *P. a. albispinus* and *P. a. sertonius* overlap widely in their morphological distributions, being discriminated only on average. Cranial and pelage characters of *P. a. minor*, such as the small skull and body, thinner guard hairs in the mid-dorsal region and the lack of an ochraceous subapical zone in the lanceolate guard hairs, are also found in juveniles of *P. a. albispinus* and *P. a. sertonius*, suggesting that the morphological differentiation of *P. a. minor* was associated with heterochronic (paedomorphic or neotenic) change during the evolution of this subspecies. Additional detailed work on the processes of growth and maturity in these taxa would contribute to an understanding of the morphological evolution of *P. albispinus*.

Key words. *Proechimys albispinus*, spiny rats, cranial size and shape variation, morphometrics, pelage and bacular morphology, subspecific differentiation.

Introduction

Echimyid rodents of the genus *Proechimys* comprise one of the most diverse, taxonomically complex and poorly understood groups of Neotropical mammals (Patton & Rogers 1983). Currently two subgenera, *Proechimys* and *Trinomys*, are recognized, with the former ranging in distribution from Nicaragua to Paraguay and the latter restricted in occurrence to eastern Brazil (Moojen 1948, Patton & Gardner 1972). Whereas the subgenus *Proechimys* is quite diverse, with some sixty named forms currently recognized (Patton 1987), only six species are recorded in the subgenus *Trinomys* (Moojen 1948, Pessôa et al. 1992, Rocha 1995).

The foundations of taxonomy of *P. albispinus* were established by Moojen (1948), who defined the limits of morphological variation in the species allocated to the sub-

genus *Trinomys* based on the survey of an array of pelage and cranio-dental characteristics. In his review of *P. albispinus*, Moojen (1948) examined population samples from the state of Bahia in northeastern Brazil and recognized two subspecies. According to Moojen (1948), *P. a. albispinus* (Is. Geoffroy, 1838) has a darker coloration on the sides of the body and a narrow skull with orthodont incisors, and occurs on Island Madre de Deus, Itaparica (near Salvador), and probably on islands in the bay of Todos os Santos and in the Paraguassú river valley, Bahia.

P. a. sertonius Thomas, 1921, has a broad skull and pro-odont incisors and is known from the type locality in Lamarâo, about 70 miles north of Bahia City (Salvador). It probably also occupies the valleys of the Jacuipe and the Itapicurú rivers and the littoral region between them.

Since Moojen's (1948, 1952) taxonomic analysis of *P. albispinus*, new data have been. accumulated on intrapopulational cranial variation (Pessôa & Reis 1992), bacular variation (Pessôa & Reis 1992, Pessôa et al. 1996), coat color variation (Pessôa & Reis 1995), morphological affinities (Pessôa et al., in press) and a new subspecies was described (Reis & Pessôa 1995).

As currently understood, *P. albispinus* ranges in distribution within the states of Sergipe, Bahia and Minas Gerais and three subspecies are recognized (Moojen 1948, Reis & Pessôa 1995). *P. a. albispinus* (Is. Geoffroy, 1838), has been known from the type locality on Ilha Madre de Deus, Itaparica (13°00' — 38°42'); we report three additional localities in Bahia. *P. a. sertonius* Thomas, 1921, has been known primarily from its type locality in Lamarâo, Ituiutaba, (11°47', 38°54'), Bahia, at an altitude of 300 meters; we now verify it from several localities in Bahia and from one locality (Cristinápolis) in the state of Sergipe. *P. a. minor* Reis & Pessôa, 1995, was recently described from Morro do Chapéu, Bahia (11°33', 41°09') at 800 meters above sea level; we report a second record in Fazenda Canoas, Juramento, Minas Gerais (16°51', 43°35') at 682 meters (fig. 1).

Moojen (1948) considered *P. albispinus* to be a species highly adapted to drier habitats, in contrast to the majority of its congeners, which are known from mesic Atlantic deciduous habitats. Indeed, the subspecies *P. a. albispinus* and *P. a. sertonius* were collected from the Caatingas biome, a type of highly deciduous forest characterized by unpredictable rainfall and semi-arid conditions, with vegetation including plants in the families Cactaceae and Bromeliaceae (Moojen 1948; Ab'Saber 1974). In contrast, *P. a. minor* was recently described from a very different habitat in the interior of the state of Bahia, located at the northern edge of the Espinhaço mountain range. This range runs approximately in a southerly direction as far as Minas Gerais. The rock formations are the result of a pre-Cambrian geosyncline, with altitudes varying from 800 to 2000 meters above sea level. Composition of plant communities is associated with altitude and soil type, from 800 to 1000 meters the vegetation is characteristically savanna, grading into grasslands between 1000 and 1100 meters. Meadows predominate in the highlands due to accumulation of organic matter (Reis & Pessôa 1995).

Our objective here was to assess the contribution of cranial morphometric size and shape variation, in conjunction with pelage and bacular qualitative data, to subspecific differentiation in *P. albispinus*. We also wanted to evaluate in a morphometric context the usefulness of the qualitative cranial traits used by Moojen (1948,
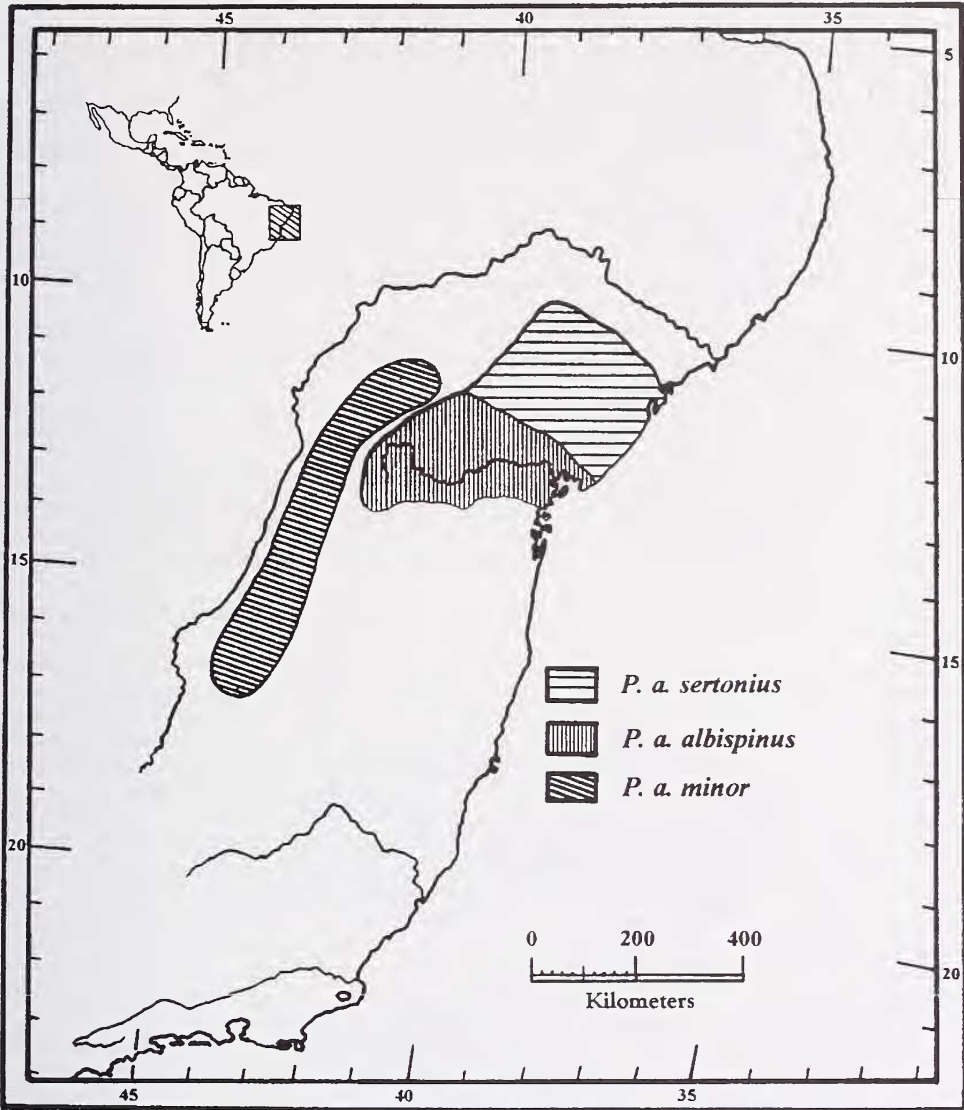
Fig. 1: Geographic range of subspecies of *Proechimys albispinus* in northeastern Brazil. Modified from Moojen (1948). *P. a. albispinus* (a) *P. a. sertonius* (s), and *P. a. minor* (m).

1952) and by Reis & Pessôa (1995) to recognize and diagnose subspecies in *P. albispinus*. We hypothesized that the cranial morphometric data should support the previous designations of subspecies that were based on qualitative pelage and skull characteristics. This study is intended to be a first step toward the understandig of patterns of variation, and their systematic and taxonomic implications, in this species.

Material and techniques

The sample analyzed here comprises a total of 133 specimens of *P. albispinus* deposited in the mammal collection of the Museu Nacional, Rio de Janeiro (U.F.R.J.) and the Museu de Zoologia da Universidade de Sâo Paulo. The specimens were identified using a combination of pelage, cranio-dental and bacular traits (Moojen 1948, Pessôa & Reis 1992), and classified in age categories defined in Pessôa & Reis (1991) on the basis of tooth eruption and surface wear criteria.

The specimens were collected at 10 localities in the states of Bahia and Sergipe in northeastern Brazil: *P. a. albispinus* from Jaguaquara (N=21), Jequié (N=21), and Vitória da Conquista (N=29); *P. a. sertonius* from Seabra (N=10), Campo Formoso (N=10), Serrinha (N=7), Feira de Santana (N=9), Senhor do Bonfim (N=6), and Cristinápolis, Sergipe (N=4); and *P. a. minor* from Morro do Chapéu (N=8).

Pelage colors were identified using the color plates of Ridgway (1912). To study bacular morphology, the phalli were removed from the adult skin and the bacula dissected from surrounding tissues under the binocular microscope.

Seventeen cranial dimensions defined in Patton & Rogers (1983), along with one additional mandibular measurement, were recorded for 133 individuals. The measurements were: greatest length of skull (GSL); basilar length (BL); palatal length (PA); zygomatic breath (ZB); alveolar length of upper tooth row (TRL); diastema (D), rostral length (RL); nasal length (NL); least interorbital constriction (IOC); rostral breadth (RB), cranial depth (CD); rostral depth (RD); maxillary breadth (MB); zygomatic breadth (ZB), length of the tympanic portion of the auditory bulla (BUL); post-palatal cranial length (PPL); length of the incisive foramen (IF); and mandibular length (ML) (fig. 2).

Because sexual size dimorphism is virtually non-existent in *P. albispinus* (Pessôa & Reis 1991), sexes were pooled for the analysis of subspecific differentiation.

Cranial character values were logarithmically transformed, and principal component analysis (PC), discriminant function analysis (DF), and size-free discriminant function analysis (SF–DF) assessed the degree of distinctiveness in cranial morphometric traits among subspecies. The logarithmic transformation preserves allometries, standardizes variances, and produces a scale-invariant covariance matrix (Jolicoeur 1963). Principal component analysis was used as an exploratory tool for summarizing multivariate patterns of variation among individuals, without the necessity of assigning individuals to taxa (Bookstein et al. 1985). The method is often of particular importance for partitioning variation in overall size and shape. Discriminant function analysis was used both to assess the degree of distinctiveness of the taxa and to identify the taxonomically useful cranial characters. This approach measures the abilities of characters to discriminate among groups (Mainly 1994, Marnell 1998), but has the disadvantage that it discriminates taxa on the basis of size, shape, or some combination of the two. To detect size-independent shape differences among subspecies, a "size-free" discriminant analysis was performed on residuals obtained by regressing each character independently against a multivariate size vector (Strauss 1985, Reis et al. 1990). All three multivariate analyses were based on the 18 x 18 covariance matrix of the log-transformed characters. All analyses and numerical figures were produced using functions written for Matlab, version 4.2c (The Mathworks 1992). Copies of these functions are available from the authors.

Results

Pelage pattern and color variation
Proechimys albispinus is easily distinguished from congeneric species, both by the joint occurrence of lanceolate and clavate guard hairs (a combination that is unique within the genus) and by the wide distribution of guard hairs on its body (Moojen 1948). A comparison of qualitative pelage features among subspecies shows that, in *P. a. albispinus*, the clavate guard hairs in the mid-dorsal region have a whitish base that gradually blackens toward the tip but is interrupted by an ochraceous-tawny
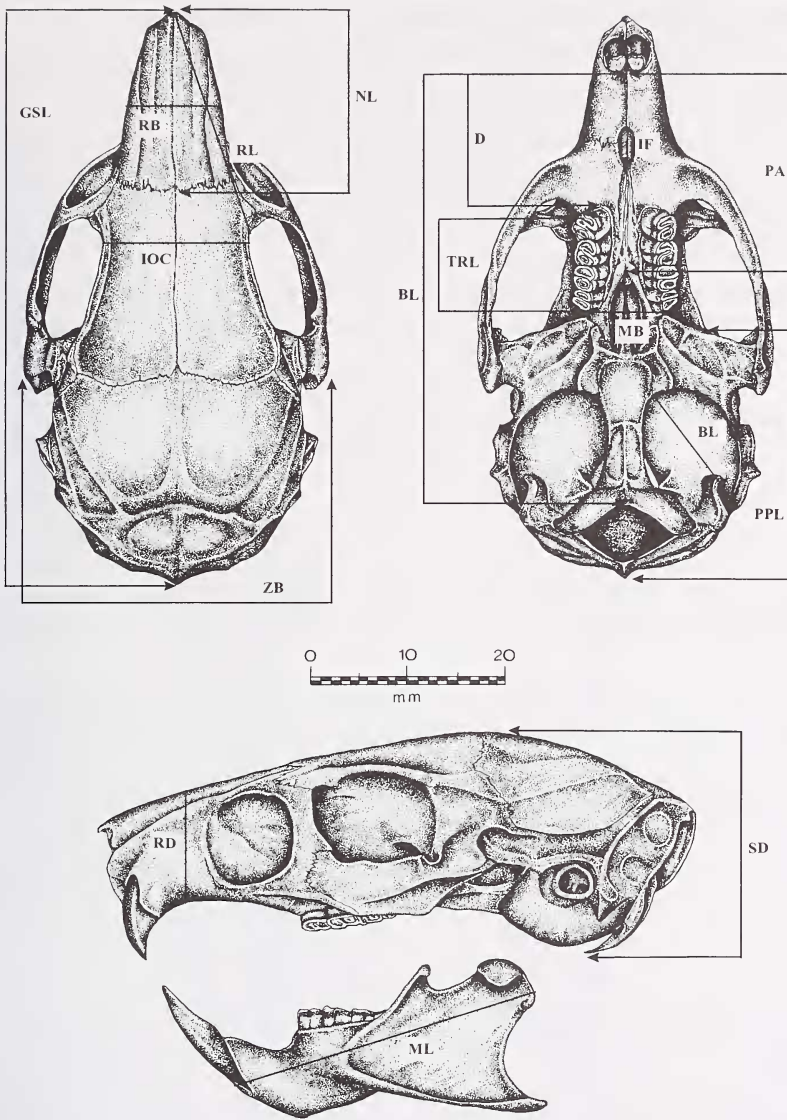
Fig. 2: Eighteen cranial measurements taken from the skulls of *P. albispinus*. See text for character abbreviations.

subapical zone (15' i in Ridgway 1912). The lanceolate guard hairs also have a whitish base that gradually blackens toward the tip, but lack a visible subapical zone. The lanceolate guard hairs vary in total length from 25 to 28 mm, with a maximum width of 1.2 mm. The guard hairs found in the outer thigh region show two patterns of coloration: one similarly having the whitish base that gradually blackens toward the

tip, and the other also gradually blackening toward the tip but with the distal fifth of the hair having an ochraceous-tawny color.

In *P. albispinus sertonius*, we found mostly clavate guard hairs with an ochraceous-tawny subapical zone in the mid-dorsal region, along with some clavate guard hairs blackened distally and lacking the subapical zone. The total length of the clavate hairs varies from 23 to 24 mm with a maximum width of 0.7 mm. The lanceolate guard hairs are whitish at the base, gradually blackening toward the tip, with a total length of 23−27 mm and a maximum width of 1.3 mm. The guard hairs present in the outer thigh region have two coloration patterns: the first pattern is whitish at the base, gradually blackening toward the tip but interrupted by a light ochraceous-buff subapical zone (color 15'b in Ridgway 1912); the second pattern is similar but lacks the subapical zone.

In *P. a. minor*, the lanceolate guard hairs in the mid-dorsal region are whitish at the base, gradually blackening toward the tip, with a total length varying from 23 to 25 mm and a maximum width of 1.0 mm. The clavate guard hairs are similarly white at their base, gradually blackening toward the tip, but interrupted by a light ochraceous-buff subapical zone (15'b in Ridgway 1912). Two patterns of coloration are found in the guard hairs of the outer thigh region: one with a whitish base, gradually blackening toward the tip, and another with a whitish base, gradually blackening toward the tip but interrupted by a buckthorn-brown subapical zone (17' i in Ridgway 1912). The guard hairs of the dorsal region in *P. a. minor* are also

Table 1: Diagnostic qualitative features of hair shape and color pattern in adults of *P. a. albispinus, P. a. sertonius* and *P. a. minor*. Color pattern includes the features of the lanceolate and clavate guard hairs in the mid-dorsal region and of guard hairs on the outer thigh.

Hair color pattern	*P. a. albispinus*	*P. a. sertonius*	*P. a. minor*
Lanceolate mid-dorsal	White base, gradually blackening toward tip	White base, gradually blackening toward tip, sometimes interrupted by ochraceous-tawny subapical zone	White base, gradually blackening toward tip
Clavate mid-dorsal	White base, gradually blackening toward tip but interrupted by ochraceous-tawny subapical zone	White base, gradually blackening toward tip, sometimes interrupted by ochraceous-tawny subapical zone	White base, gradually blackening toward tip but interrupted by a buckthorn-brown subapical zone
Guard hair outer thighs	White base, gradually blackening toward tip, sometimes with an ochraceous-tawny distal fifth zone	White base, gradually blackening toward tip but interrupted by a light ochraceous-buff subapical zone	White base, gradually blackening toward tip but interrupted by a light ochraceous-buff subapical zone

thinner than in *P. a. albispinus* and *P. a. sertonius*, giving a less spiny appearance to the pelage. Table 1 summarizes the differences of the color pattern of hairs on the mid-dorsal and outer thighs in the subspecies.

Dental traits and bacular shape
Comparison of qualitative dental traits among subspecies shows that *P. a. sertonius* and *P. a. minor* differ from *P. a. albispinus* in having pro-odont incisors and only one counterfold in the molariform teeth, as opposed to having orthodont incisors and the fourth premolar with two counterfolds instead of one.

Qualitative analysis of the bacular morphology among subspecies does not show any significant differences in size or shape. The baculum in the three subspecies has a dorsoventral curvature and slightly tapered lateral indentations near the mid-shaft. The proximal end is paddle-shaped and pointed. The distal end has well-developed apical wings with a pronounced medial depression. Figure 3 shows a dorsal and ventral view of a baculum of *P. albispinus*, which characterizes the general morphology of the three subspecies.
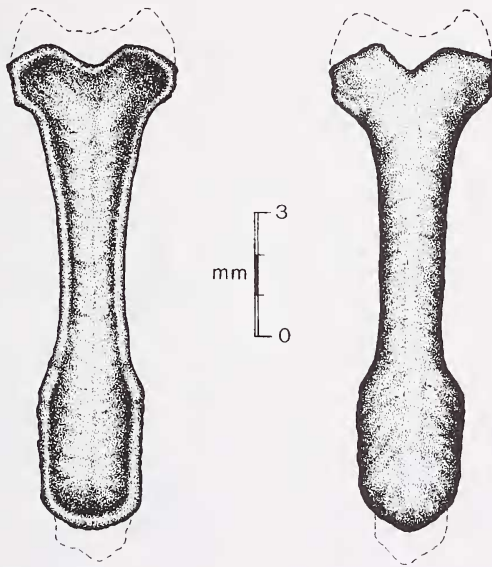

Fig. 3: Dorsal and ventral view of bacula of *Proechimys albispinus* that characterize the general morphology in the three subspecies. Solid lines represent bone, dotted lines represent cartilage.

Cranial morphometric variation
The principal component analysis (fig. 4A, B) of the pooled samples describes the major patterns of size and shape variation. The first principal component (PC1) accounts for 48.8 % of the total variation among all characters (fig. 4A), and was interpreted to be a general size vector because the correlation of all cranial characters with PC1 were positive and approximately of the same high magnitude ($r = 0.5-0.9$, $P < 0.01$; fig. 4B). This multivariate measure of overall skull size is highly correlated
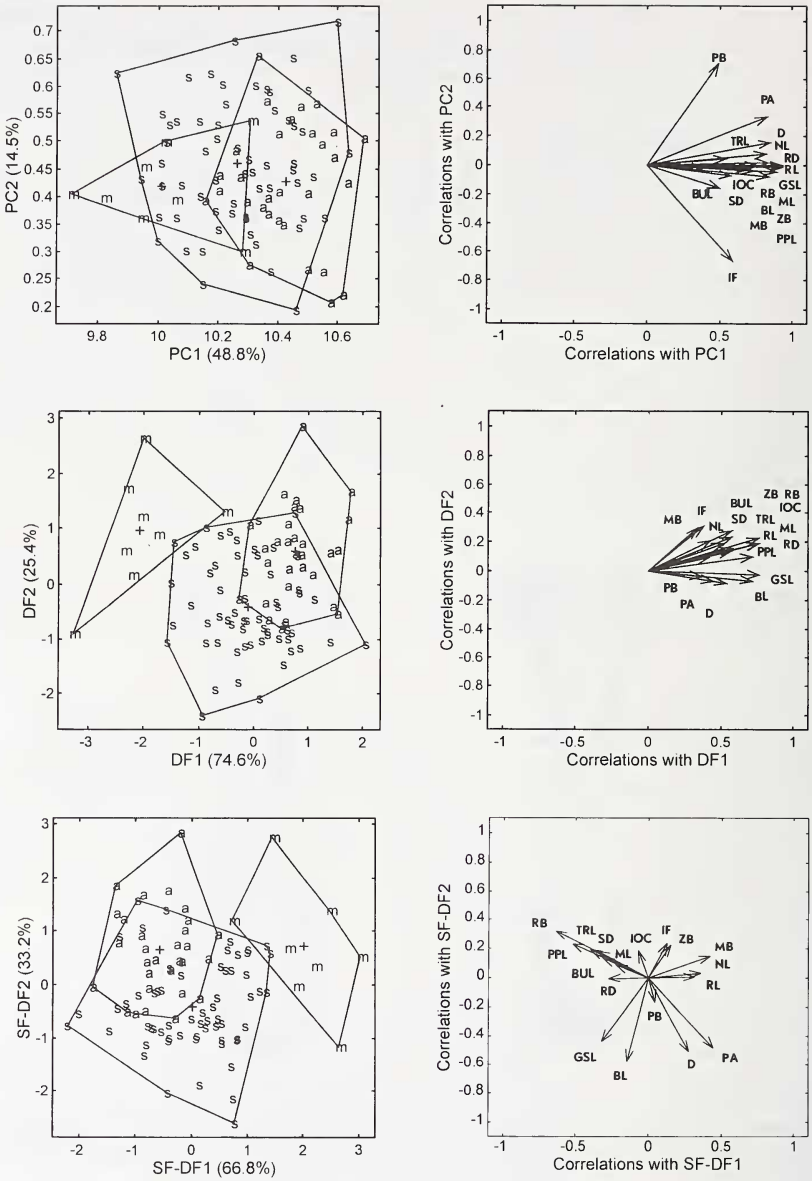
Fig. 4: Bivariate plots (A, B, C) and vector plots (D, E, F) of the projection scores of individuals of three subspecies on the first and second principal components (PCs), discriminant functions (DFs) and size-free discriminant functions (SF–DFs), respectively, for subspecies of *P. albispinus*: *P. a. albispinus* (a), *P. a. sertonius* (s) and *P. a. minor* (m).

with greatest skull length, a commonly used univariate measure of skull size (r = 0.92, P<0.01). The subspecies are aligned in a cline of increasing cranial dimensions (fig. 5).

Craniometric differences among subspecies of *P. albispinus* were initially assessed by discriminant function analysis (fig. 4C, D). The first two discriminant functions together account completely for the total among-group variation (DF1 accounting for 74.6 % and DF2 accounting for the remaining 25.4 %). The projection of individual discriminant scores for the three subspecies samples of *P. albispinus* on the plane defined by DF1 and DF2 reveals two major almost distinct clusters (fig. 4C). One cluster is represented by samples of *P. a. albispinus* from three different localities in Bahia and of *P. a. sertonius* from six localities in Bahia and Sergipe. Individuals of these samples overlap extensively in the multivariate character space, indicating that they are morphometrically very similar. The second cluster represents a single population of *P. a. minor* from Morro do Chapéu, characterized by low scores on DF1. However, this axis must also be interpreted as a general size vector because the correlation of all cranial characters with DF1 were all positive and approximately of the same high magnitude ($r = 0.5-0.9$, $P<0.01$; fig. 4D). Thus, because adults of *P. albispinus* show substantial amounts of variation in cranial size within populations due to indeterminate growth (Pessôa & Reis 1991), the differences
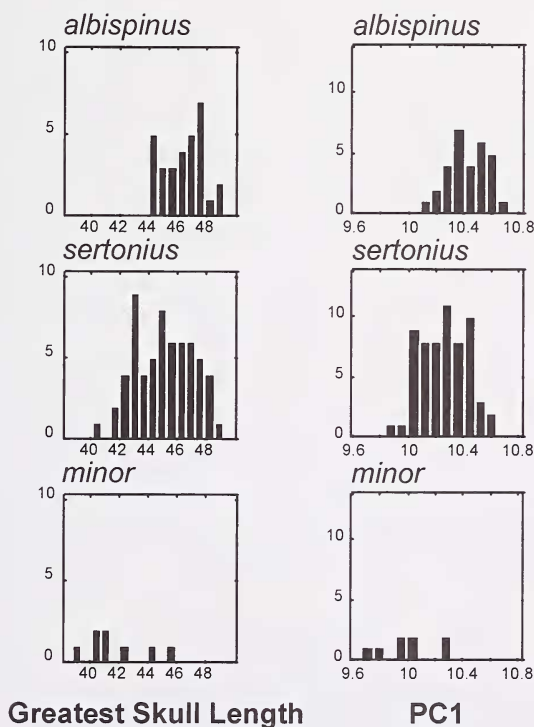

Fig. 5: Histograms of two measures of skull size (columns of panels) for the three subspecies of *P. albispinus* (rows of panels): greatest skull length (a univariate measure), and the scores of individuals on the first principal component (PC1, a multivariate measure).

portrayed by the discriminant analysis confound aspects of both size and shape variation.

We performed the additional size-free discriminant analysis (fig. 4E, F) in order to assess differences in cranial shape among subspecies. The first size-free function (SF–DF1) accounted for 66.8 % of the total variation and was interpreted as a shape differentiation axis because of the great contrast in correlations among the cranial characters (fig. 4F). As with the preceding discriminant analysis (fig. 4C), *P. a. minor* is almost completely discriminated from the other two subspecies. However, in this case the discrimination is based on shape variation: individuals of *P. a. minor* have relatively longer incisive foramina, relatively greater nasal and rostral lengths, and relatively broader maxillary and zygomatic arches. Although the *P. a. albispinus* and *P. a. sertonius* samples overlap widely, they have a mean shape difference along SF–DF2, indicating that individuals of *P. a. albispinus* have relatively larger bullae and longer post-palatal length, broader interorbital and rostral widths, and a deeper skull. *P. a. sertonius* has a relatively longer skull, basilar length, diastema and palate (fig. 4F).

Discussion

Recognized subspecies of *P. albispinus* have been characterized primarily on the basis of a combination of pelage-coloration and qualitative dental traits, but are difficult to objectively diagnose based on these criteria because these characters can be age-dependent. In addition, recurrent cranial morphologies, which appear in subspecies from other locations and are associated with substantial amounts of intra-populational variation in qualitative traits of skull and pelage, render the definition of subspecific units difficult. The lack of unique, discrete character states that clearly diagnose the subspecies of *P. albispinus* has undoubtedly contributed to the difficulty of assessing levels of differentiation, isolation, and systematic relationships. Variation of color patterns in subapical zones of guard hairs, which has traditionally been used for the diagnosis of subspecies, is quantitative and subtle. Although differences are apparent, by themselves they are not diagnostic, and the same is true for qualitative aspects of bacula and skull shape.

In his revision, Moojen (1948) described the color and thickness of guard hairs and provided descriptions of several qualitative aspects of skull and dental morphology for each subspecies of *P. albispinus*. These qualitative characters included: (1) size and shape of bulla, (2) degree of development of ridges and depth of the jugal bone, (3) degree of development of the post-orbital process of the zygomatic arch, (4) shape and anatomy of the incisive foramen, (5) placement of the posterior palatine foramen, (6) extension of the mesopterygoid fossa, (7) number of counterfolds in the molariform teeth and (8) condition of the incisors. Although Moojen (1948) described variation in pelage and these qualitative aspects of the skull, he found diagnostic features to define subspecific units of *P. albispinus* primarily in a subset of these (thickness and color patterns of guard hairs, patterns of counterfolds in molariform teeth, and incisor morphology) and used this combination of traits to characterize *P. a. albispinus* and *P. a. sertonius*. For comparative purposes, Reis & Pessôa (1995) described *P. a. minor* based on the same set of characters although they stressed its smaller cranial and body size and lack of visible ochraceous subapical

zone in the mid-dorsal guard hairs. The morphometric characters used in this study were intended to quantify many of the same aspects of the cranial form characterized by Moojen (1948) and Reis & Pessôa (1995).

We originally hypothesized that the cranial morphometric data would support the previous designations of subspecies based on pelage and qualitative aspects of the skull observed by Moojen (1948). The morphometric analyses partially supported our preliminary hypothesis in that they permit the almost complete discrimination of *P. a. minor* from the other two subspecies on the basis of cranial shape, but *P. a. albispinus* and *P. a. sertonius* overlap widely in their morphological distributions being discriminated only on average. However, some of the subspecific differences we observed have contradicted Moojen's (1948) diagnoses. For example, Moojen described the bulla of both *P. a. albispinus* and *P. a. sertonius* as small and smooth, while our morphometric analysis indicated that the size of the bulla is relatively larger in *P. a. albispinus* than in both *P. a. sertonius* and *P. a. minor.* Moojen, based on a little sample, described the skull to be narrow in *P. a. albispinus* and broad in *P. a. sertonius*, but now with an increased sample, our analysis supports a different conclusion.

Two aspects of the ordination of taxa allocated to *P. albispinus* are noteworthy and deserve further comments. First, although our samples of *P. a. albispinus* and *P. a. sertonius* were all collected from localities in the Caatinga habitat, Moojen (1948) noted that the localities where the taxa were collected differ somewhat in detail. *P. a. sertonius* were collected from "typical" Caatinga forest, a climax of mainly deciduous trees, whereas *P. a. albispinus* was collected from climax forest having a moderate proportion of deciduous trees. This small difference in habitat is correlated with the small difference in cranial morphology between the taxa.

In contrast, *P. a. minor* occurs in a very different habitat, in which the composition of plant communities is associated with altitude and soil type, and from altitudes of 800 to 1000 meters the vegetation is characteristically savanna. It may be that the characters found to discriminate *P. a. minor* in multivariate space (e. g., relatively larger mandible and rostrum, relatively smaller rostral breadth, tooth-row length, and post-palatal length) are correlated with habitat differences. In addition, cranial and pelage characters of *P. a. minor,* such as small skull and body size, thinner guard hairs in the mid-dorsal region and the lack of an ochraceous subapical zone on the guard hairs, are also found in juveniles of *P. a. albispinus* and *P. a. sertonius*. We hypothesize that the morphological differentiation of *P. a. minor* was caused by a heterochronic (paedomorphic or neotenic) change during the evolution of this sub-species. Additional detailed work on the processes of growth and maturity in these taxa would contribute to an understanding of the morphological evolution of *P. albispinus*.

Zusammenfassung

Die unterartliche Differenzierung von *Proechimys albispinus* ist bisher aufgrund der erheblichen Varianz in den bewerteten Merkmalen und der teilweise schwierigen Feststellung der Merkmalausprägung nicht befriedigend geklärt. In dieser Untersuchung wurden 18 Schädelmerkmale (Abmessungen, Form) bei drei Unterarten von insgesamt 10 Fundorten ermittelt und die Werte einer Hauptkomponenten-Analyse, einer Diskriminanzfunktion und einer größenunabhängigen Diskriminanzfunktion unterzogen. Ebenso wie in der von Moojen (1948) publizierten Unterartgliederung, die im wesentlichen auf Fell- und Schädelformmerkmalen beruht, ließ sich in dieser Untersuchung *P. a. minor* anhand der Schädelform deutlich von den beiden anderen Unterarten *P. a. albispinus* und *P. a. sertonius* unterscheiden, für diese beiden untereinander gelingt dies jedoch nicht so gut. Typische Merkmale von *P. a. minor* wie relativ geringere Schädel- und Körpergröße, dünnere Deckhaare im mittleren Rückenbereich sowie weitere Merkmale der Deckhaare finden sich auch bei Jungtieren der beiden anderen Unterarten, so daß ein genaues Verständnis der Evolution der Körpermerkmale der drei Unterarten noch weiterer Untersuchungen bedarf.

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